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COMPARATIVE ENERGETICS DURING EARLY DEVELOPMENT OF TWO MARINE FISH SPECIES, *SOLEA SENEGALENSIS* (KAUP) AND *SPARUS AURATA* (L.)

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Summary

Growth, energy content, ingestion and respiration rates and energetic efficiencies were measured in the larvae of two marine fish (*Solea senegalensis* and *Sparus aurata*) whose eggs have a similar diameter (approximately 1 mm) and energy content (approximately 1 J), but whose larvae reach a quite different mass after the first month of life. Experiments were carried out in populations reared under the same conditions in the laboratory during the first month after hatching. *Solea senegalensis* grow from hatching to the start of metamorphosis (approximately day 14) at twice the rate of *Sparus aurata* (specific growth rate for *Solea senegalensis* 0.25 μg day^{-1}; specific growth rate for *Sparus aurata* 0.12 μg day^{-1}). The tissues in *Solea senegalensis* larvae accumulated energetic reserves that were used during metamorphosis, which occurred during the third week after hatching. Ingestion and respiration rates differed in the two species during the experimental period. Although *Solea senegalensis* continued eating during metamorphosis, the specific ingestion rates decreased during the process. Nevertheless, no great differences in specific ingestion rates and rates of oxygen consumption were observed when comparing the same larval mass range. Larvae of both species showed an allometric relationship between respiration rate and biomass. The energetic efficiencies calculated in the present study denoted different metabolic patterns in each species. In *Solea senegalensis*, the energy used for growth increased progressively during the larval (pelagic) period and then, from the first signs of metamorphic transformation, remained almost constant. In this species, the energy allocated to growth was greater than that allocated to metabolic processes. *Sparus aurata* invested less energy in growth than in metabolic processes and displayed a constant energy allocation throughout the experimental period. During the first month after hatching, *Solea senegalensis* always allocated more energy for growth than did *Sparus aurata*.

Key words: fish, larva, larval growth, energetic efficiency, ingestion rate, respiration rate, Senegal sole, *Solea senegalensis*, gilthead seabream, *Sparus aurata*.

Introduction

Embryonic development, the start of feeding and larval growth in the early stages of marine fish are greatly affected by biotic and abiotic conditions. Thus, the rate of mass gain and the duration of the larval period depend on factors such as water temperature and food availability. Nevertheless, there is also a noticeable interspecific variability in the ontogeny and larval development among sympatric species. A good example of such variability can be observed when comparing the soleid Senegal sole (*Solea senegalensis* Kaup) and the sparid gilthead seabream (*Sparus aurata* L.). Both species occur throughout the northeastern Atlantic Ocean and the Mediterranean Sea (Bauchot and Hureau, 1986; Quéro et al., 1986), and their distribution areas overlap along the Atlantic coast of the Iberian Peninsula and in the western basin of the Mediterranean Sea. The spawning seasons of these species partially coincide during late winter and early spring, at least in the Gulf of Cádiz (Arias and Drake, 1990). Gilthead seabream larvae start to feed on day 4 after hatching, when the yolk sac is completely exhausted, and metamorphosis occurs gradually during the second month of life, after which the juveniles continue their pelagic way of life. In contrast, Senegal sole larvae start to feed on day 2 after hatching, when 5 % of the yolk reserves remains, and metamorphosis occurs by approximately the third week after hatching. During this rapid transformation, the larvae lose their bilateral symmetry and change swimming plane, acquiring the typical morphology of flat fish changing from a pelagic to benthic mode of life.

Although there is very little information about these larval stages in nature, rearing procedures in the laboratory for both species are similar and well standardised during the first stages of development. Both species spawn eggs with a similar diameter (approximately 1 mm) and energy content (approximately 1 J) (Pascual and Yúfera, 1993; Yúfera et al., 1999). However, under similar rearing conditions, it is usual

to obtain gilthead seabream larvae of around 500–700 µg dry mass (*DM*) with a 15–20 % survival rate at the end of the first month of culture, while Senegal sole larvae reach a dry mass of 2000–2500 µg and show a survival rate of over 80 % during the same period. These similarities in the starting conditions and differences in the potential for growth provide a chance to compare the two patterns of development from the point of view of the transformation of matter and energy. Some aspects of metabolism during the egg, yolk and first feeding phases in these species have been examined in previous studies (Parra et al., 1999; Yúfera et al., 1999; Parra and Yúfera 2000). In the present study, the energetic balance and the energy allocation during the first month of larval development of the two species have been measured under laboratory conditions to examine the mechanisms that control differential growth in larval marine fish.

Materials and methods

Eggs of *Sparus aurata* (L.) and *Solea senegalensis* (Kaup) were obtained by natural spawning from captive broodstocks and were incubated at 19.5 °C. Newly hatched larvae were transferred to 300 l tanks with sea water supplied from a well at a constant temperature of 19.5±1 °C and a salinity of 33 ‰. Constant slight aeration and continuous illumination were provided. Initial larval density ranged from 50 to 70 larvae l^{-1}. From day 3 to day 15, approximately 15–20 % of the water volume was renewed daily, and approximately 200 % was renewed daily from day 15 onwards. In *Sparus aurata*, the rotifers *Brachionus rotundiformis* and *B. plicatilis* (at 10 ml^{-1}) were given as live food for 11 days of exogenous feeding starting on day 4 after hatching. In *Solea senegalensis*, *B. plicatilis* (at 10 ml^{-1}) were supplied for 4 days starting on day 2 after hatching. After this, both fish species were fed with *Artemia* nauplii (at 2 ml^{-1}) until the end of the experiment. These are the same experimental conditions that we have used in previous studies with these species. Larval growth and changes in energy content, ingestion rate and respiration rate were studied in both species over the first month of development.

Growth, ingestion and respiration patterns were obtained from pooled data using different egg batches obtained over several years. Larvae for analyses were sampled periodically during the experimental period and anaesthetised with 200 p.p.m. of ethyl-4-amino-benzoate. Body dry mass was determined by drying samples of approximately 15–30 larvae at 85 °C to constant mass. The accuracy of the method was previously checked by comparison with freeze-dried samples. Specific growth rate (*G*) was calculated as the slope of the exponential regression of larval body dry mass on time. Energy content was determined using a semimicro bomb calorimeter (Parr 1421) using samples weighing approximately 20 mg. Three subsamples per determination were used in each case. Energy employed in growth (G_e) was calculated using the larval energy content and the daily dry mass increase. Mouth width (W_m) and total length (*TL*) in Senegal sole larvae during development were measured as described by Hunter (Hunter, 1981) and Yúfera et al. (Yúfera et al., 1993a) respectively. The W_m pattern as a function of *TL* in Senegal sole was compared with data for gilthead seabream taken from Fernández-Díaz et al. (Fernández-Díaz et al., 1994).

Ingestion rate of fish larvae was determined directly in the rearing tanks. Ingestion during the rotifer-feeding period was determined using the method of Yúfera et al. (Yúfera et al., 1993b) and Parra and Yúfera (Parra and Yúfera, 2000). Approximately 20–30 larvae were sampled periodically (every 5, 10 or 15 min) over a period of 2 or 4 h depending on larval age, and then anaesthetised with ethyl-4-amino-benzoate. The larvae were examined under a light microscope to examine the gut contents. This method is based on the use of green-coloured rotifers by means of a short re-feeding period in a dense suspension of microalgae cells. These green rotifers can be distinguished from those that have been in the rearing tanks for several hours, because the latter appear brown. The fullness of the gut follows an asymptotic function:

$$C = C_{max}(1 - e^{-bT}), \quad (1)$$

where *C* is the number of green rotifers (per larva showing gut contents), C_{max} is the asymptote of the curve (rotifers $larva^{-1}$), *T* is time (h) and *b* is a regression parameter that indicates the instantaneous rate of gut filling (h^{-1}). This model was fitted by the iterative method to the asymptotic function. The ingestion rate (*I*) was calculated as the derivative of this function against time at the starting point, when no green rotifers had yet been evacuated:

$$I = C_{max}b. \quad (2)$$

During the *Artemia*-feeding period, the ingestion rate was calculated from the decrease in prey density (Yúfera and Rodríguez, 1987) using the equation:

$$I = DC_x/L, \quad (3)$$

where *D* is the decreasing rate of prey number in the water calculated as the slope of the exponential regression of prey density on time, C_x is the geometric mean of the initial and final prey concentrations and *L* is the density of larvae in the water.

In both cases, ingestion rate was expressed as dry mass ingested per larva per day, *I* (µg $larva^{-1}$ day^{-1}). Values of rotifer dry mass and energy content used for the calculations were determined as a function of the egg/female ratio observed in the larval gut (Yúfera et al., 1997). The dry mass and energy content of recently hatched *Artemia* nauplii were calculated in the present study (dry mass 2.5±0.2 µg; energy content 21.3±0.2 J mg^{-1}; means ± S.D., *N*=3). The energy ingested (I_e) was calculated from the ingestion rates and the energy content of the prey.

Rates of oxygen consumption ($\dot{V}_{O_2}$) were measured in a respiratory chamber equipped with a polarographic oxygen sensor. The electrode was attached to a dissolved oxygen meter (Strathkelvin Instruments model 781b with 1302 oxygen electrode). The output was wired *via* a data-acquisition board

Table 1. *Description of the energetic efficiencies*

Efficiency	Derivation	Description
K_1	G_e/I_e	Gross growth efficiency
K_2	$G_e/(G_e+M_e)$	Net growth efficiency
A	$(G_e+M_e)/I_e$	Assimilation efficiency
M_1	M_e/I_e	Gross metabolic efficiency
M_2	$M_e/(M_e+G_e)$	Net metabolic efficiency

G_e, energy used in growth; I_e, the energy ingested; M_e, the energy used in metabolic processes.

(Metrabyte DAS8-PGA) to a PC program used for continuous data logging. The Weiss equation was used to estimate oxygen solubility with respect to temperature and salinity (Weiss, 1970). After a 5–15 min equilibration period, the electrode stabilised, and oxygen concentration declined at a constant rate. $\dot{V}_{O_2}$ was estimated as the slope of the regression line of oxygen concentration on time for 1–2 h following electrode stabilisation. Sterilised and air-saturated sea water (salinity 33‰) was used. The respiratory chamber was kept at a constant temperature of 19.50±0.05 °C in accordance with the temperature of well water used for larval rearing studies in our Institute from 1986. The water volume in the respiratory chamber was chosen according to the number and size of the larvae and ranged between 3 and 5 ml. The larvae were held without food in the chamber, but they had been held under normal rearing conditions in the tanks prior to measurements. When the larvae died inside the chamber, the data were excluded. $\dot{V}_{O_2}$ was calculated in nmol O_2 larva^{-1} h^{-1}. The energy expended in metabolic processes (M_e) was calculated using $\dot{V}_{O_2}$ and the oxycalorific coefficient (13.56 J mg^{-1} dry mass; from Brett and Groves, 1979) for conversion into energy units. Energetic efficiencies were calculated using the energy ingested (I_e), the energy employed in growth (G_e) and the metabolic energy (M_e) (Table 1).

In all cases, polynomial regressions were fitted to energetic data as a function of age or mass. The maximum power of the polynomial functions with statistical significance was chosen following the method described by Zar (Zar, 1984).

Results

Larval growth in Senegal sole during the experimental period is presented in Fig. 1A. Larval dry mass data were fitted to two exponential curves in accordance with two differentiated developmental stages (Fernández-Díaz et al., 2001). The first regression line shows the growth from first feeding to 14 days after hatching during the pelagic stage, while the second regression line shows the growth from 14 days after hatching until the end of the experiment. Daily growth rates (G) were 0.245 and 0.127 day^{-1}, respectively. Most *Solea senegalensis* larvae initiate metamorphosis approximately 14 days after hatching, and at 17 days after hatching most larvae have completed eye migration and lie on the bottom of the tank. We have used an intermediate value of 0.186 to estimate G_e during the transition between the two growth rates (13–15 days after hatching) to avoid an unrealistic

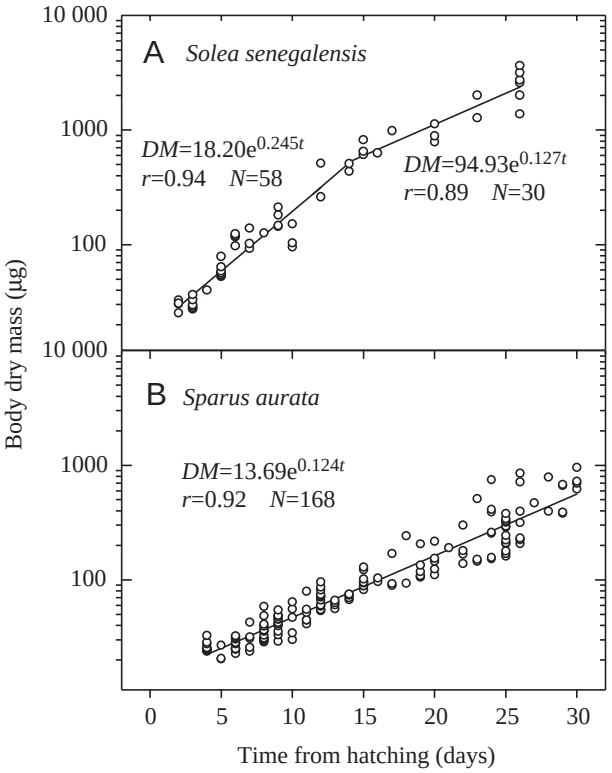

Fig. 1. Changes in dry mass during larval development for (A) *Solea senegalensis* and (B) *Sparus aurata*. *DM*, larval body dry mass (µg); *t*, time (days); *r*, correlation coefficient; *N*, number of samples.

overestimation. Larval growth in *Sparus aurata* is shown in Fig. 1B. In this case, the data were fitted to only one exponential curve, and the growth rate was 0.124 day^{-1}. The mouth width of Senegal sole larvae increased linearly with the increase in total length (Fig. 2). The linear regression line fitted to the data lies above that for gilthead seabream (from Fernández-Díaz et al., 1994) over the entire larval length range.

The energy content of sole larvae was minimal at the onset of feeding (approximately 19 J mg^{-1}) and increased to a maximum (approximately 23 J mg^{-1}) by 12–14 days after hatching, when eye migration began. The energy content then decreased, reaching values of approximately 20.5 J mg^{-1} by the end of eye migration (Fig. 3). In gilthead seabream, the energy content increased initially up to 20 J mg^{-1} by 15 days after hatching and then decreased slightly, reaching values of approximately 19 J mg^{-1} by the end of the experimental period (Fig. 3; Table 2).

The ingestion rate (I; µg larva^{-1} day^{-1}) of Senegal sole increased progressively with the increase in larval mass from the beginning of growth (Fig. 4A). Nevertheless, this increase was not continuous: it slowed between 100 µg and 1000 µg dry mass and then increased again. In gilthead seabream, I increased continuously with larval dry mass (Fig. 4B), although the incrementing slope tended to decrease gradually. Data were fitted to a polynomial function in each case. The equations used to determine the energy ingested (I_e) in both species are shown in Table 3.

Table 2. *Equations describing changes in energy content as a function of larval age in* Solea senegalensis *and* Sparus aurata *larvae*

Species	Equation	*r*	*N*
Solea senegalensis	$EC=-2.64\times10^{-5}t^5+2.26\times10^{-3}t^4-6.95\times10^{-2}t^3+0.91t^2-4.59t+26.40$	0.91	9
Sparus aurata	$EC=-1.14\times10^{-5}t^5+1.05\times10^{-3}t^4-3.61\times10^{-2}t^3+0.56t^2-3.75t+26.80$	0.94	10

EC, energy content ($J\,mg^{-1}$); *t*, time from hatching (days); *r*, correlation coefficient; *N*, number of mean values.

Table 3. *Equations describing changes in ingestion rate as a function of the larval body dry mass in* Solea senegalensis *and* Sparus aurata *larvae*

Species	Equation	*r*	*N*
Solea senegalensis	$\log I=0.67\log DM^3-5.17\log DM^2+13.55\log DM-9.55$	0.89	30
Sparus aurata	$\log I=-0.78\log DM^2+4.63\log DM-3.84$	0.92	168

I, ingestion rate ($\mu g\,larva^{-1}\,h^{-1}$); *DM*, larval body dry mass (μg); *r*, correlation coefficent; *N*, number of samples.

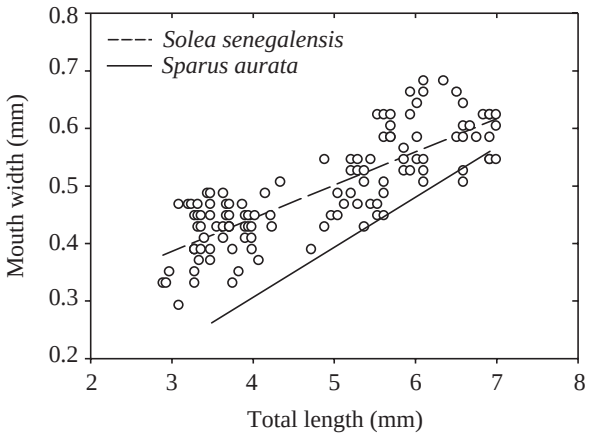

Fig. 2. Mouth width with respect to total larval length for *Solea senegalensis* and *Sparus aurata*. *TL*, total length (mm); W_m, mouth width (mm). *Sparus aurata* data are taken from Fernández-Díaz et al. (Fernández-Díaz et al., 1994). For *Sparus aurata*, $W_m=0.044+0.088TL$; $r=0.95$; $N=113$. For *Solea senegalensis*, $W_m=0.214+0.057TL$; $r=0.67$; $N=119$.

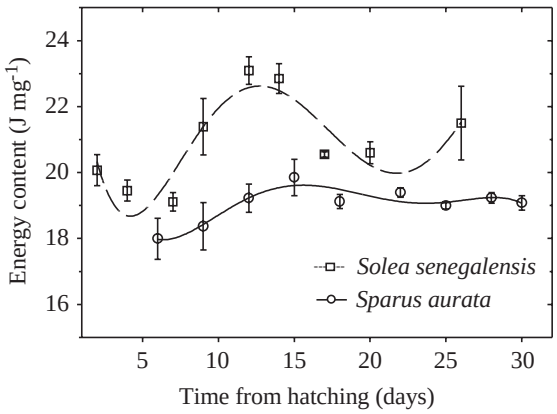

Fig. 3. Energy content ($J\,mg^{-1}$) of *Solea senegalensis* ($N=3$) and *Sparus aurata* ($N=3$) larvae during the first month after hatching. Values are mean ± S.D.

In Senegal sole, changes in $\dot{V}_{O_2}$ ($nmol\,O_2\,larva^{-1}\,h^{-1}$) with respect to larval dry mass showed the same pattern as the ingestion rate (Fig. 5A). The incrementing slope decreased when larval dry mass ranged from approximately 100 to 1000 µg. Data obtained over the entire experimental period were fitted to a polynomial function (Table 4). From the beginning of feeding until larval dry mass reached 150 µg, $\dot{V}_{O_2}$ values were also fitted to a power function, the slope of which was 1.06 (Table 4). In gilthead seabream, $\dot{V}_{O_2}$ values were fitted to a power function and showed a similar trend over the entire experimental period (Fig. 5B; Table 4). As above, the curves presented in Table 4 were used to determine the energy allocated to metabolism (M_e) in both species.

Gross growth efficiency (K_1), assimilation efficiency (A) and gross metabolic efficiency (M_1) patterns in Senegal sole with respect to dry mass are shown in Fig. 6. All the efficiencies (K_1, A and M_1) decreased during the first stages of development; after a minimum at approximately 100–200 µg dry mass, they increased progressively, reaching the highest values between 1500 and 2000 µg dry mass, after which they decreased again. Over the entire period, the gross growth efficiency (K_1) was always higher than the gross metabolic efficiency (M_1). Gilthead seabream also displayed an initial decrease in efficiencies (K_1, A and M_1), but a slight increase in efficiencies occurred above 200 µg dry mass (Fig. 7B). In contrast to Senegal sole, the gross growth efficiency (K_1) was always lower than the gross metabolic efficiency (M_1). As the maximum dry mass of gilthead seabream during the experimental period was 560 µg, values of the efficiencies in Senegal sole have also been plotted over the same range of dry mass to provide a better comparison of the two species (Fig. 7A). The initial trend is similar in both species, but Senegal sole showed higher K_1 and A values than gilthead seabream. The metabolic efficiencies (M_1) were constant (approximately 10–12 %) in both species in individuals weighing 100–560 µg (Fig. 7A,B).

Table 4. *Equations describing changes in oxygen uptake rate as a function of larval dry mass in* Solea senegalensis *and* Sparus aurata *larvae*

Species	Period	Equation	*r*	*N*
Solea senegalensis	A	$\log\dot{V}_{O_2}=0.48\log DM^3-3.51\log DM^2+8.92\log DM-6.05$	0.94	58
	B	$\dot{V}_{O_2}=0.360DM^{1.06}$	0.87	21
Sparus aurata	A	$\dot{V}_{O_2}=0.486DM^{0.992}$	0.95	99

A, over the entire experimental period; B, in individuals weighing 20–150 μg.
$\dot{V}_{O_2}$, rate of oxygen consumption (nmol O_2 $larva^{-1}$ h^{-1}); *DM*, larval body dry mass (μg); *r*, correlation coefficient; *N*, number of samples.

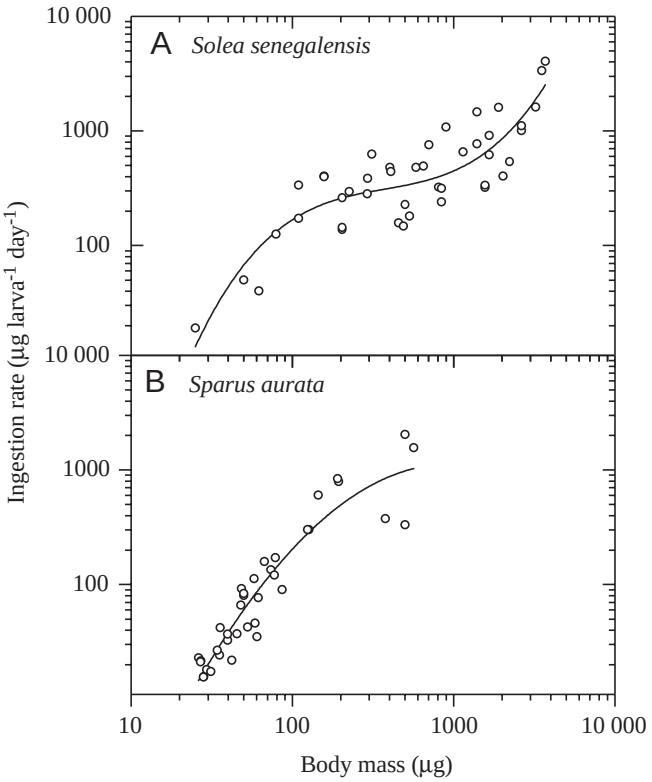

Fig. 4. Ingestion rate (*I*; μg $larva^{-1}$ day^{-1}) as a function of larval body dry mass for (A) *Solea senegalensis* and (B) *Sparus aurata*.

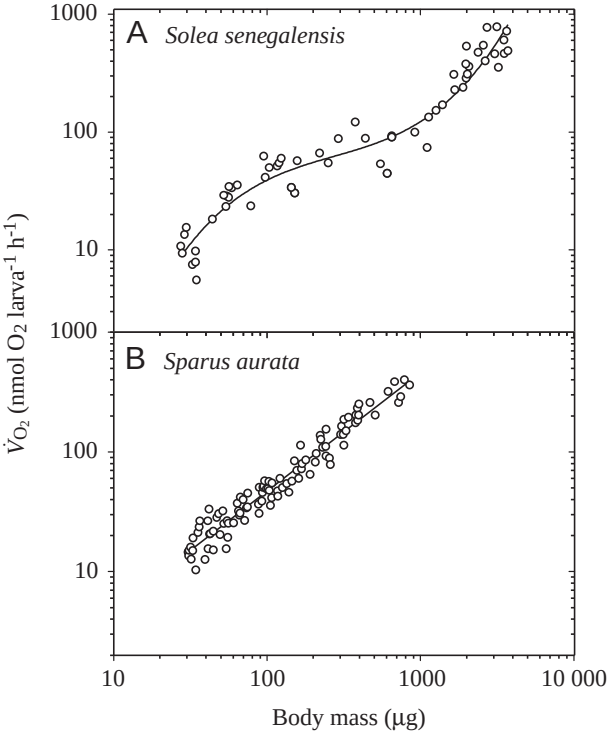

Fig. 5. Rates of oxygen uptake rate ($\dot{V}_{O_2}$; nmol O_2 $larva^{-1}$ h^{-1}) as a function of larval body dry mass for (A) *Solea senegalensis* and (B) *Sparus aurata*.

The net growth efficiency (K_2) and net metabolic efficiency (M_2) indicate the amount of the assimilated energy that is used in growth and in metabolic processes, respectively. These efficiencies for Senegal sole varied over the experimental period (Fig. 8A). At first feeding, sole larvae allocated a similar amount of energy to growth and to metabolic processes, but the energy used for growth increased progressively during the first days of feeding and growth. Above a dry mass of 200–300 μg, just before metamorphosis started, the efficiencies remained almost constant, with 65–70 % of this energy being allocated to growth and 30–35 % to metabolic processes. In contrast, the gilthead seabream showed an almost constant allocation of assimilated energy over the entire experimental period, allocating approximately 35 % of this energy to growth and 65 % to metabolic processes (Fig. 8B).

Discussion

As expected, the two species exhibited different growth patterns during the first month. *Sparus aurata* showed a constant growth rate throughout this period. The growth rate obtained in the present study (0.12 day^{-1}) is close to values reported in other studies under laboratory conditions (Tandler and Helps, 1985; Yúfera et al., 1993a). Gilthead seabream prolong their larval period over the 2 first months of life (Person-Le Ruyet and Verillaud, 1980) and, although gastric glands and acid digestion appear by the fifth week, scales and definitive juvenile anatomical features appear gradually during the second and third month (M. Yúfera, unpublished data). In contrast, *Solea senegalensis* showed a growth rate of 0.25 day^{-1} during the larval period that was almost twice that observed in gilthead seabream. In *Solea senegalensis*, growth rate decreased to 0.13 day^{-1} when the larvae started

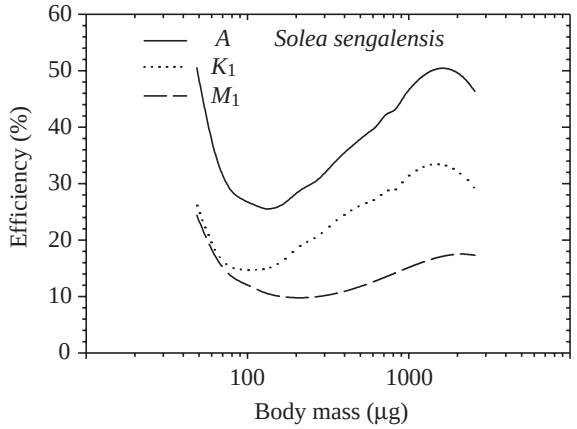

Fig. 6. Patterns of gross growth efficiency (K_1), assimilation efficiency (A) and gross metabolic efficiency (M_1) as a function of larval body dry mass for *Solea senegalensis*.

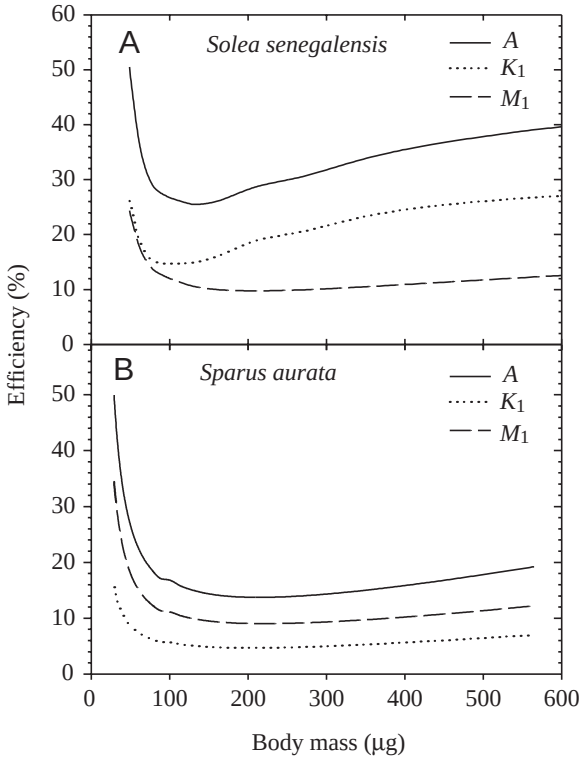

Fig. 7. Patterns of gross growth efficiency (K_1), assimilation efficiency (A) and gross metabolic efficiency (M_1) for (A) *Sparus aurata* and (B) *Solea senegalensis* larvae with a dry mass of less than 600 µg.

metamorphosis by day 14 after hatching, although the completion of eye migration and the change to a benthic habit occurred by 18–20 days after hatching, after which acid protease activity starts to increase (Martínez et al., 1999). Nevertheless, gastric glands and acid digestion in the Senegal sole appear by the end of the first month of life (Martínez et al., 1999; Ribeiro et al., 1999).

The ingestion pattern during the first month was also

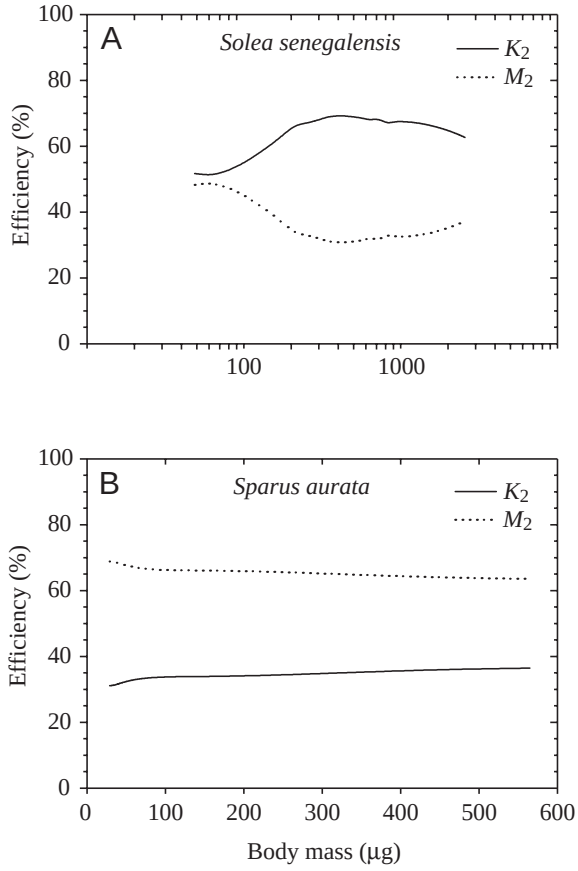

Fig. 8. Patterns of net growth efficiency (K_2) and net metabolic efficiency (M_2) as a function of larval body dry mass for (A) *Solea senegalensis* and (B) *Sparus aurata*.

different in the two species. Nevertheless, both species exhibited a similar trend when compared over the same range of larval dry mass. Surprisingly, the amount of ingested matter for a given larval size was always lower in Senegal sole. Although some flatfish species stop feeding during metamorphosis (Tanaka et al., 1996), Senegal sole continue to eat during the transformation, but the total daily amount ingested remains almost constant during this stage in spite of the fact that the body continues to grow. The slight decrease in specific ingestion rate is compensated by the energetic reserves that have been accumulated during the larval period. After the start of feeding, the carbon content and energy content of the larval tissues of Senegal sole increase progressively and reach relatively elevated values for marine fish larvae (Yúfera et al., 1999). The present study shows that these reserves are used during metamorphosis. A decrease in carbon, energy and lipid content in larval tissues during the transformation has been observed in *Pleuronectes platessa* (Christensen and Korsgaard, 1999) and in other species (Youson, 1988). Senegal sole start feeding earlier and feed faster than gilthead seabream. A few hours after the opening of the mouth, all sole larvae from the same egg batch are eating, whereas seabream larvae require several days to reach 100 % feeding activity in the population (Parra and Yúfera,

2000). In addition, sole larvae possess an anatomical feature that appears to be of primary importance to mass gain, a wider mouth, which allows them to ingest larger-sized prey and, consequently, to obtain a higher energy input per prey item consumed. Therefore, the energetic balance between expended and ingested energy during the process of catching and ingestion is more favourable for Senegal sole than for gilthead seabream during early development.

Gilthead seabream and Senegal sole are species that live in temperate habitats. During the larval stages, both species grow continuously in the presence of prey. In contrast, several hours of starvation causes an immediate cessation of growth and poor larval health. In the absence of prey, the larvae tend to retain ingested food in the gut. Therefore, respiration experiments were performed with individuals with gut contents, and we assumed that our measurements represented routine metabolic rate plus specific dynamic action. This metabolic status is assumed to be continuous in larvae under rearing condition (Parra and Yúfera, 2000).

The metabolic rate ($\dot{V}_{O_2}$) of gilthead seabream larvae during the first month of life increased isometrically with larval mass (mass exponent b=0.99). This value is quite close to that found in *Sparus aurata* larvae by Quantz and Tandler (Quantz and Tandler, 1984) and by us in a previous study (Parra and Yúfera, 2000). It has been suggested that this exponent is close to unity in the early stages of development of marine fish larvae (Wieser, 1995), although reported values in different species are quite variable (Walsh et al., 1989; Oikawa et al., 1991). In juveniles and adults, this relationship between metabolic rate and body mass is allometric, and the mass exponents for regression of metabolic rate on body mass are usually less than 1. This decrease is associated with a progressive increase in mass of structural tissues with low metabolic activity (bones, scales, etc.) (Oikawa et al., 1991; Segner et al., 1994). Brett and Groves (Brett and Groves, 1979) suggested that the average value for this mass exponent in fish was 0.86. In Senegal sole, the metabolic rate during the pelagic period also scales isometrically with body mass (b=1.06), as has been reported for the closely related species *Solea solea* (Day and Jones, 1996). However, the value of b calculated for *Solea senegalensis* with a dry mass of 150–1500 μg does not correspond with those of larvae and adults. The relatively low metabolic demand observed during all or part of metamorphosis could be a way to save energy. This kind of response has also been described for *Pseudopleuronectes americanus* during metamorphosis (Laurence, 1975) and for *Paralichthys olivaceus* (Kurokura et al., 1995). Although not as pronounced as in flatfish, a switch in metabolic demand during early development at the beginning of metamorphosis has also been observed in other fish species (Appelbaum and Kamler, 2000). This pattern of energy allocation allows Senegal sole larvae to develop the differentiation processes associated with metamorphosis and to continue growing, even with a lower energy intake per unit of biomass. Nevertheless, a limitation in energy intake prevents growth and the completion of transformation (Fernández-Díaz et al., 2001).

Houde and Zastrow (Houde and Zastrow, 1993) reported average values of approximately 30 % for K_1 and 60 % for A in fish larvae. However, there is inter- and intra-specific variability. In the present study and above a larval mass of 100 μg, K_1 ranged from approximately 15 to 35 % in *Solea senegalensis* and from 4 to 7 % in *Sparus aurata* and A ranged from 35 to 52 % in *Solea senegalensis* and from 14 to 20 % in *Sparus aurata*. Such values are, in general, low because the larvae were being reared under conditions of high prey density (Parra and Yúfera, 2000). The initial decline in K_1 and A later switched to an increase, describing a U-shaped trend in relation to larval mass, during early development prior to metamorphosis. This pattern for K_1 has also been observed in other fish larvae (Houde and Schekter, 1983; Yamashita and Bailey, 1989) and has been associated with changes in the ingestion rates and in the cost/benefit relationship of energy uptake (Checkley, 1984; Kiørboe et al., 1987; Theilacker, 1987; Tucker, 1989).

In the present study, the larvae of both species were reared under satiation conditions and under similar conditions of prey density to remove, as far as possible, the influence of feeding conditions. There was, however, some variation in the feeding regime because *Artemia* nauplii were offered earlier to sole larvae, although in terms of larval mass the difference was relatively small (80 μg dry mass in sole larvae compared with 90 μg dry mass in seabream larvae). In any case, considering the difficulties of measuring and simulating the potential optimum feeding conditions of larvae in nature, the approach has been to provide the best possible feeding conditions for each species in a realistic way to compare larvae growing in the laboratory. It is obvious that feeding behaviour and ability also differ in the two species, as explained above. This fact probably contributes to differences in the energy expended in searching for and handling prey and may, consequently, explain the differences in energy allocation.

In addition, survival during the first month was not considered in the calculation of biomass production. Therefore, the estimates presented here have to be considered at an individual level and out of an ecological context in which mortality by predation and prey quality and availability are important aspects of the metabolic response of a larval fish population. In any case, it is evident that Senegal sole invest more energy in growth than do gilthead seabream during the first developmental stages. It is worth noting that the percentage of assimilated energy used for growth is always higher than that used for metabolic processes in *Solea senegalensis* and that the opposite is true for *Sparus aurata* (Fig. 7). Such variability in food conversion efficiency in larvae of species sharing resources and environmental conditions has also been observed in other species (Kneib and Parker, 1991).

There are some methodological constraints in the present study. As pointed out above, it is difficult to define and measure the routine metabolic rate of small fish larvae eating continuously. They have a high basal energy expenditure and low metabolic scope (Wieser and Medgyesy, 1990; Wieser,

1995). Faeces and energy expenditures in searching for food and in eating were not measured and were not considered in the calculation of assimilation efficiency. Therefore, the possible causes of the difference in K_1 between Senegal sole and seabream require some consideration. After the opening of the mouth, larvae of both species exhibit low swimming activity. Sole larvae become progressively more active during the first days of feeding up to the point when they acquire a benthic habit and settle on the bottom 2 weeks later. Conversely, seabream larvae show active prey-searching behaviour only from approximately day 10 onwards. The same swimming behaviour was observed during the respiration experiments. Energy expenditure in searching tends to decrease with increasing prey concentration (Laurence, 1977). In the present study, under conditions of high prey density, feeding success depends largely on encounter opportunity rather than on searching effort. In addition, the energy expended in swimming and sucking during attack is very low compared with the energy supplied by the prey (Drost and van der Bogaart, 1986), although the gain in energy evidently increases with the size and energy content of the prey eaten. Therefore, although not measured, there could be assumed *a priori* to be some differences in foraging effort between the two species, but not excessive differences. Perhaps the main difference lies in the slow acquisition of prey-searching behaviour in seabream larvae, as explained above.

The other relevant factor involved in assimilation efficiency concerns the digestion process. Several studies indicate that growth and assimilation efficiencies decrease at high consumption rates (Boehlert and Yoklavich, 1984; Theilacker, 1987). Furthermore, marine fish larvae, like other plankton-feeders, show a range of feeding behaviours between two extreme strategies: (i) maximisation of ingestion with a short residence time in the digestive tract and a relatively low assimilation rate, or (ii) a low rate of ingestion with a long residence time in the gut and a high assimilation rate. Obviously, this point cannot be considered independently of the previous one because, under the same conditions of prey density, an increase in the number of ingested prey items would imply greater energy expenditure. Seabream larvae belong to the first group, and live rotifers within the gut and faeces could be easily observed during routine rearing. There are few observations for sole larvae, but it is a reasonable possibility that a relatively higher assimilation rate occurs. Only a more detailed study of the different compartments of metabolism and feeding physiology will answer these questions.

Both species start their development with similar amounts of energetic reserves, but after 30 days Senegal sole can weigh up to five times more than gilthead seabream under the same rearing conditions. Differences occurred over the entire experimental period, but mainly during the first 2 weeks. In that period, feeding behaviour and physiological processes promote fast development and growth in Senegal sole. Thus, Senegal sole are more efficient than gilthead seabream even during the endogenous feeding period, showing a higher efficiency of conversion of yolk into larval tissue (Yúfera et al., 1999). After the start of feeding during early development, sole larvae show a higher predatory capacity than seabream larvae, i.e. they are able to ingest larger prey and they presumably have a higher metabolic efficiency given the above-mentioned assumptions. This greater efficiency in utilizing the ingested energetic resources, and not a higher specific ingestion rate, is the main reason for the fast larval growth of the Senegal sole in comparison with the gilthead seabream.

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